THE PRESENT STATUS OF LEDERMANN'S APRIL RIVER LOCALITIES IN PAPUA NEW GUINEA

W. Takeuchi

Botanical Research Institute of Texas
Research Associate, PNG National Forest Service
c/o Lae Herbarium and PNG Forest Research Institute
P.O. Box 314
Lae, Morobe Province 411, PAPUA NEW GUINEA

M. Golman

Divisional Manager, PNG National Forest Authority
PNG National Forest Service
P.O. Box 5055, Boroko, NCD
PAPUA NEW GUINEA

ABSTRACT

The April River of East Sepik Province has received little attention since the German explorations of the early 1900s. However the social, logistical, and vegetation status of April environments present considerable opportunities for floristic discovery and documentation.

KEY WORDS: botanical survey, Kaiserin-Augusta Expedition, type localities, Papua New Guinea.

ABSTRACT (JAPANESE)

その生物史上のユニークな価値にもかかわらず、東セピック州のエイプリルリバー地域は、ドイツ人による最初の探検以来わずかにしか注目されてこなかった。 セピック川流域の、史学的に価値がある地域を調査するにあたっては、まず現状を知ることが重要である。そこで、最近の調査によって得られた、社会的状況、各種調査を行うための諸々の環境や植生に関する概要を発表する。本調査結果から当地域は植物学上の発見や新たな考証が行われる可能性が非常に高いということがうかがえる。

TOK IGO PAS (MELANESIAN TOK PISIN)

April wara long Is Sepik Provins i bin kisim liklik luksave tasol long taim bilong Geman long 1900 ikam inap long nau. Tasol, bikos long dispela hap, igat bikpela na gutpela bus, diwai, graun na tu laif bilong ol man na meri ino gat bikpela senis, wei dispela i bringim ol saveman na meri long lukluk moa long wok painim out igo insait long ol bus na diwai long hap bilong April wara.

INTRODUCTION

Of all the exploratory surveys conducted in New Guinea during the last 100 years, the German Kaiserin-Augusta Expedition of 1912–13 stands out as being particularly significant. During that expedition, botanist Carl Ledermann traveled extensively through the south Sepik basin with a multidisciplinary contingent, eventually collecting a total of 6,639 angiosperm numbers over a period of 18–19 months. Originating at an early point in the exploration of the Papuasian flora, a disproportionate number of Ledermann's collections were designated as type specimens. Many of his localities have never been revisited. The unfortunate circumstances of Ledermann's labors are an enormous obstacle to modern scientific inquiry, for the main German sets were destroyed in the

1943 fire at Berlin Herbarium, effectively erasing the primary basis for the identification of numerous plant species. Veldkamp et al. (1988) have provided an informative discussion of the relevant issues surrounding the loss of such a critical botanical corpus.

One of the most productive parts of the Kaiserin-Augusta itinerary was the series of collecting trips made by Ledermann to the April River (Aprilfluss). The Aprilfluss yielded a bountiful harvest of new species, many of which have unfortunately proven impossible to evaluate without the original collections. With modern assessment indicating the apparent existence of a zone of floristic endemism centered on the Hunstein-April region, it has become particularly desirable to revisit the classical localities and secure new material. Such efforts would enable neotypification of many species whose types were lost at Berlin (e.g., *Tapeinochilos hollrungii* K. Schum.; cf. Gideon 1998). Although a list of plants requiring new collections is reportedly being compiled (Veldkamp et al. 1988), no summaries are yet available.

The first serious reexamination of Ledermann's sites occurred in 1966, with the CSIRO-sponsored expedition to Mt Hunstein by R. Hoogland and L. Craven. In 1989 a multi-institutional survey returned to the Hunstein Range under the auspices of the National Geographic Society, obtaining 1,200 more botanical numbers (cf. Bakker 1994 for a general account). The first author, one of five botanists on that expedition, independently returned to the Hunstein summit in July–August 1990 and to the nearby Waskuk Hills in August 1994 and June 1995. Additional collections from the April-Sitipa drainages were made in September 1990, and from the April River serpentine zone on the south side of Mt Hunstein, in July 1995 (Fig. 1). The most recent trip to the subdistrict occurred in August 2001 (cf. Takeuchi & Golman 2002; Takeuchi & Renner 2002), from which much of the information in the following narrative has been taken.

THE SOCIAL ENVIRONMENT

The indigenous population of the Hunstein subdistrict is spread diffusely through the region in small clan-based villages. Ambunti is the largest settlement; with a district headquarters, tradestores, an aid post, two schools, several churches, and a grass airstrip. Further upriver and within the April catchment, the average settlements are much smaller, often consisting of a single extended family. At Garuka (Waskuk Hills) for example, the total adult population was exactly ten during the time of the 1995 survey. The larger villages like Baglam and Melawei have about a hundred inhabitants.

In the Sepik region, river-borne traffic is the major means of communication, trade, and transport. Most of the population are thus concentrated near the water. This also affords the people convenient access to fish and saksak (made from the starchy pith of the *Metroxylon* palm) which together comprise the bulk of the average villager's diet. A limited amount of subsistence slash and

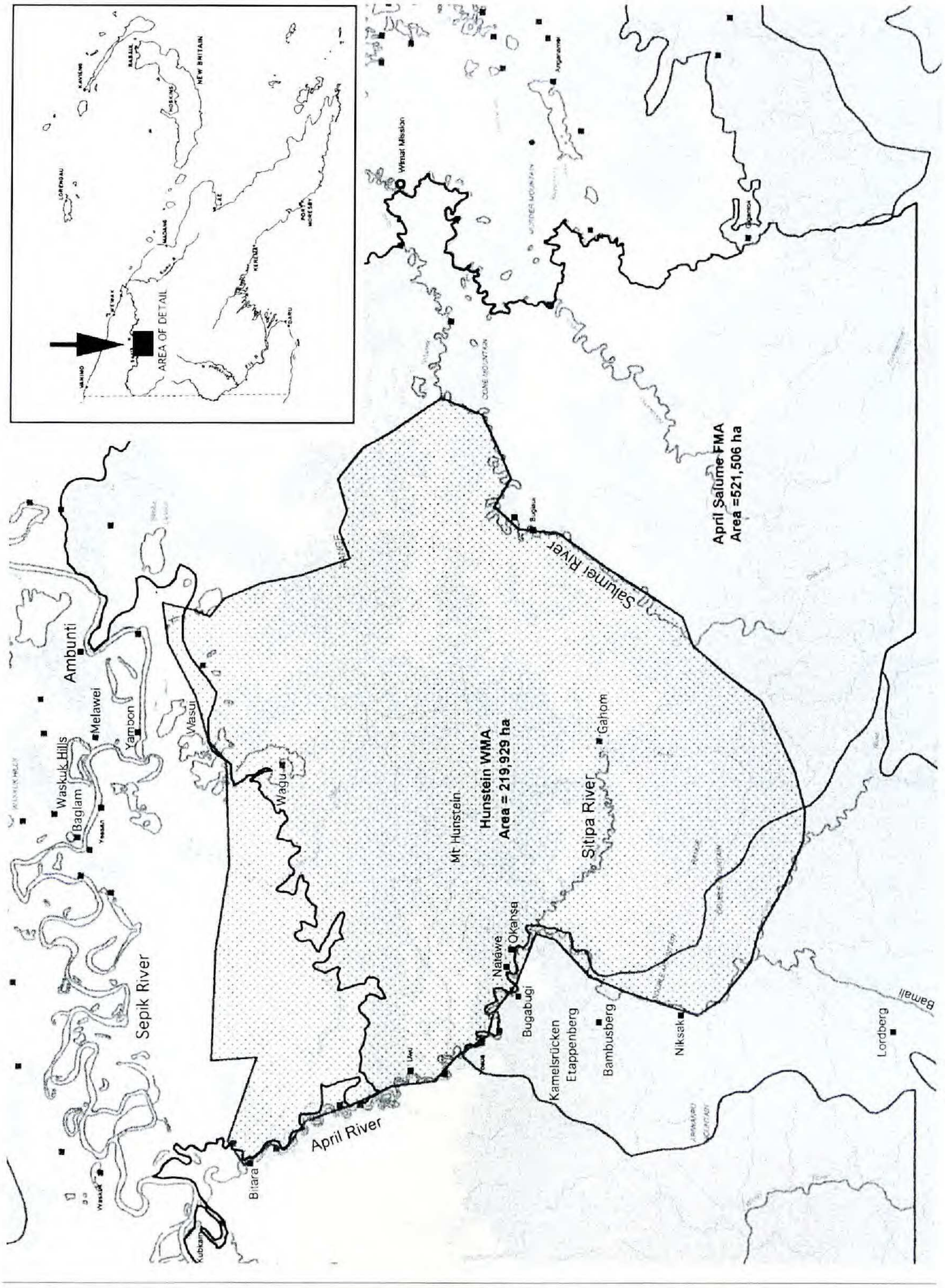

FIG. 1. Principal localities from the Hunstein subdistrict. Scale 1:500,000. The April Salumei FMA (Forest Management Agreement) Area is a proposed logging concession. Inset shows location of the Hunstein tract.

burn gardening provides dietary variety. Sweet potatoes, taro, bananas, and coconuts constitute the main crops, but plantings are generally not a principal source of village sustenance. For the most part, the April River populace are semi-nomadic hunter-gatherers.

Like the Sepik River, the April is a meandering silt-laden waterway which often changes course after severe floods. A recently introduced fish from South America (the pacu, erroneously identified as a piranha in the local media) has now entered the April drainage and is rapidly becoming the most commonly caught fish for consumption. Villagers report that the appearance and proliferation of the pacu have been accompanied by disappearance of many native fish species, particularly the endemic species of Sepik catfish (*Arius* spp., cf. Allen 1991). The pacu has reportedly been involved in several fatal attacks on bathers, but such anecdotal reports are often exaggerated and their veracity is uncertain.

Socioeconomic development in the April region is virtually nonexistent. The local economy is primarily subsistence in nature, and cash incomes are opportunistic. Money is occasionally earned from the sale of wood carvings, crocodile skins, birdwing butterflies, cacao, and from seasonal sources in the ecotourism niche market. Very recently, a lucrative trade has also emerged involving *Gyrinops ledermannii* Domke (Thymelaeaceae), with Indonesian buyers paying up to PNGK 800–1,000 (USD 265–335) for each kg of black wood. The arborescent species is endemic to the upper Sepik (Ding Hou 1960), and has become a significant income source for landowners due to consumer demand for the wood's pleasing fragrance, a development reminiscent of the sandalwood trade. Known as 'may-hasei' in the Parenemo language, *G. ledermannii* is common on the southwest side of Kamelsrücken and is also distributed on slopes facing the April River, particularly near Etappenberg (Takeuchi & Golman 2002). For many decades the species was known only by Ledermann's type gathering from the May River, but current indications suggest the tree probably ranges even into West Papua (ibid.).

In spite of income from such incidental sources, by Western standards the overall status of the people would be regarded as impoverished. Due to the inaccessibility of health services, mortality rates are high, especially from malaria and infections, and the local inhabitants frequently seek palliatives and remedies from whatever natural resources are at hand. Skin diseases like ringworm and scabies often affect entire villages.

April River culture is an improbable assortment of incongruities and apparent contradictions. Villagers have adopted western standards of dress, yet still retain their traditional lifestyle and customs. Many of the residents speak standard English, often freely intermixed with their tribal tokples (Baihenemo, Parenemo, Waskukil) in ad hoc combination. Although Christianity in its many variants is dominant throughout the region, belief in sorcery is closely interwoven through the Christian ethic. Sudden deaths are nearly always attributed

to black magic or to secret murders (sanguma) facilitated by plant poisons. 'Ukhop pok' (*Anodendron oblongifolium* Hemsl.; Apocynaceae) is the most commonly mentioned agent in sanguma killings. There is also a widespread conviction in the existence of spirits (masalai), believed to pervade all aspects of the natural world and which form an inseparable part of the villagers' metaphysical world-view.

The population growth rate for East Sepik Province is currently 2.9% per annum, a relatively high figure, but below the Mamose[1] regional average of 3.3% (National Statistical Office 2001). Most of the provincial population is concentrated in the built-up areas near the coast, and the interior sections such as April River consist primarily of wilderness habitat. Due to the low population densities in this part of PNG, there are no subsistence-based threats to the environment. However, because the entire region along the April-Salumei is one of PNG's most economically depressed areas, landowners are understandably attracted by the inducements offered by logging and mining interests. A major portion of the district has been proposed as a timber concessional area under the Forest Management Agreement protocols (cf. Papua New Guinea Forest Authority 1998). Reconciling the conflicting desire for socioeconomic development on one hand, with conservation concerns on the other, will be a major challenge for community planners. Many of the relevant issues are presently being addressed by the World Wildlife Fund (WWF), through the establishment of an ICAD (Integrated Conservation and Development) program in the Hunstein area and the related demarcation of a Wildlife Management Area (WMA; Fig. 1). The Village Development Trust is also contemplating start-up of a comparable program in the Bugabugi territory and the Waskuk Hills (Aung & Kisokau pers. comm.). In the past, investigators moved freely throughout the area, subject only to approval from the customary landowners. With the recent and impending developments, this is likely to change. Intervention by nongovernment organizations (NGOs) invariably results in new requirements which can complicate scientific access and research. The complications are offset however, by the real and perceived benefits which NGO association can deliver to affected communities.

Land ownership and the subsequent control of access to forest resources are traditional and patrilineal. Nearly all territories fall under clan jurisdiction, so discretion must be exercised during plant collecting in order not to trespass on land unapproved for gathering. A gratuity paid to the landowner(s) is often necessary to ensure approval for plant collecting.

THE LOGISTICAL ENVIRONMENT

In contrast to the many obstacles which confronted the first explorers, access to the upper Sepik has improved to such an extent that the region is now a major

[1]Mamose is the administrative unit composed of West Sepik, East Sepik, Madang, and Morobe Provinces.

ecotourist destination. Until recently, ocean-going tourist vessels made regularly-scheduled luxury cruises as far upstream as Ambunti. Although travelers can still expect numerous delays arising from conditions endemic to developing countries, entry to the April basin has been considerably eased by the new airfields at Bugabugi and Niksak.[2] Both airfields are small grass strips maintained by New Tribes Mission, and can accept only the single-engine Cessna 206, with maximum lift capacity of 5 passengers or 400 kg. Otherwise access can also be made via the airfield at Ambunti, which can accommodate larger twin-engined Islanders capable of carrying 19 passengers or 1,600 kgs of freight (Missionary Air Fellowship). From Ambunti a visitor would ordinarily proceed to the April River with dugout canoes powered by Yamaha outboard motors (15, 30, or 40 hp motors are the usual ratings). The fuel consumption of a 30 hp motor on a roundtrip between Ambunti and Bugabugi will be at least 140 liters. In the upper Sepik, fuel is problematic, being either unavailable or prohibitively expensive.

The buttress ridges in the vicinity of Bugabugi (Pinape, Natawe, and Okahsa), lead directly to Mt Hunstein and represent the easiest path to the top. In 1989, the National Geographic expedition approached the summit from the north, which is actually the longest and most logistically difficult land route. Ledermann's two trips to Hunsteinspitze had come the same way, from Ambunti and through Wasui-Wagu Lagoon (cf. Steenis-Kruseman 1950: 317–18). The entry via Wagu was similarly taken by Hoogland and Craven in 1966 (Craven pers. comm.). The quickest access however, is to follow the south-descending ridges from the April River, preferably starting at Natawe (Fig. 2). With the newly operational airfield at Bugabugi, the latter route can now be used to reach the Hunstein crestline within two days of departure from the provincial seat at Wewak. The south-side approach provides the added advantage of passage through unexplored ultrabasic habitats.

Field conditions in the April drainage are onerous. The heat and humidity are stultifying during dry periods and the wet season is accompanied by torrential downpours after which the river is hazardous at many places along its course. Prolonged visits are a health risk. The physical difficulties are aggravated by the absence of any service infrastructure throughout the region, except for basic facilities at missionary stations. Over much of the year the mosquito and leech populations are exceptionally troublesome even by the standards of an alluvial tropical environment. When it is not raining, horseflies are annoyingly plentiful, especially in areas where pigs are present in the forest. Poisonous snakes have been responsible for a substantial number of deaths in the village communities.

---

[2]Niksak is 18 km north of Lordberg, one of the enigmatic localities from Ledermann's Aprilfluss itinerary on the Bamali tributary, and would be the only cost-effective point of access in any future attempt at revisiting the latter site.

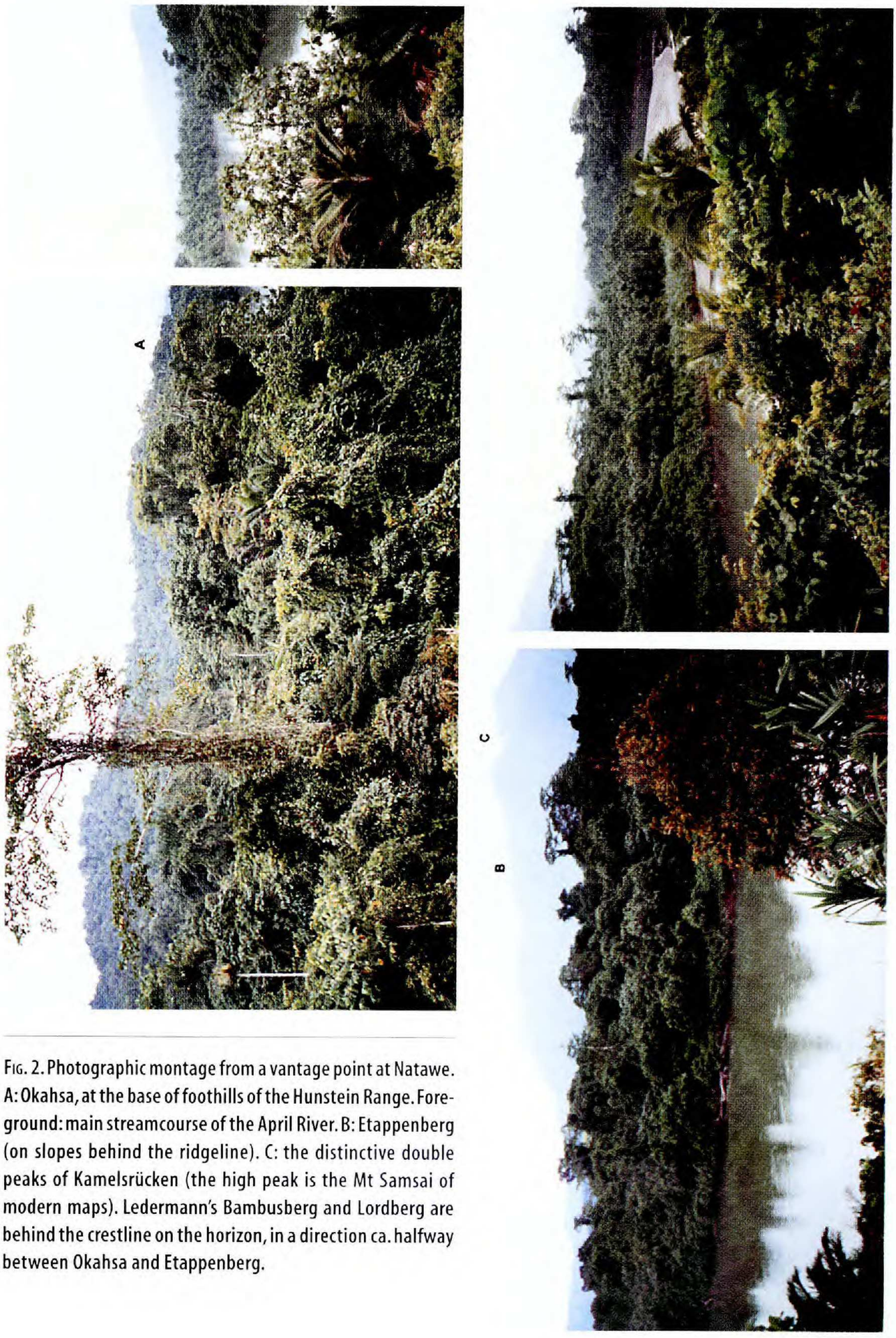

FIG. 2. Photographic montage from a vantage point at Natawe. A: Okahsa, at the base of foothills of the Hunstein Range. Foreground: main streamcourse of the April River. B: Etappenberg (on slopes behind the ridgeline). C: the distinctive double peaks of Kamelsrücken (the high peak is the Mt Samsai of modern maps). Ledermann's Bambusberg and Lordberg are behind the crestline on the horizon, in a direction ca. halfway between Okahsa and Etappenberg.

THE FLORISTIC ENVIRONMENT

The vegetation along the April River consists of three principal formations. The swamp forest (with several facies including levee forest, meander scrolls, swales, etc.) is the dominant community on the flood plain. Typically waterlogged or inundated during rainy periods, the swampy habitat is dominated by *Metroxylon sagu* Rottb., *Campnosperma brevipetiolata* Volk., or herbaceous vegetation (especially *Saccharum robustum* Brandes & Jeswiet ex Grassl; cf. Warner & Grassl 1958). On better drained alluvium the forest is more structurally developed, giving rise to a second association with many macrophyllous taxa (e.g., *Artocarpus communis* J.R. & G. Forst., *Caryota rumphiana* Mart., *Pangium edule* Reinw., *Sterculia macrophylla* Vent., and *Nauclea orientalis* L.). These communities have characteristically high proportions of robust climbers along the edges, particularly *Calamus*, *Korthalsia*, and to a lesser extent *Freycinetia*, and the interior sections often support a luxuriant shrub layer. On the Hammermaster and Saunders (1995a, b) forest classification system, the riverine vegetation is described as an open forest on low elevation plains and fans, or as swamp woodland (forest code 'Po' and 'Ws' on overlays SB 54-4 and SB 54-3 to the Ambunti and Mianmin 1:250,000 Australian Survey Corps topographic sheets). Paijmans (1976) provides a concise overview of the vegetation in such environments.

At several places along its course, the April River skirts the base of serpentine/ultramafic foothills and there is a sharp floristic break as the swamp and alluvial associations are replaced by foothill forest. The contrasting features of the forest facies on ultramafics are: 1) a pronounced reduction in climbers (e.g., *Calamus* is virtually absent), 2) a more varied canopy structure, including a noticeable reduction in large-leaved taxa, 3) increased floristic richness, most apparent in an understory which is not subject to the periodic flooding characteristic of the alluvial flats, 4) a 'clean' visual aspect to the community, with good visibility through the forest because of the absence of climbers and comparative lack of epiphytic growth on tree boles, 5) a very obvious change in taxonomic composition, many taxa being common on the ultramafic slopes but absent from immediately adjacent alluvial forest. When observed from the outside, the ultramafic community is similar in physiognomy and structure to a montane forest, except for the paucity of epiphytes. Based on air photo interpretation, the April foothill zone is a medium-crowned low altitude upland forest (code 'Hm' in Hammermaster & Saunders 1995a), a vegetation type which is probably Papuasia's richest forest structural category (Louman & Nicholls 1995). Although an unpublished report (Sohmer et al. 1991) provides a brief botanical description of the Hunstein Range, there is still nothing in the way of a comprehensive account for the April basin.

The forest on ultramafic foothills is easily accessed near Bugabugi[3] (Pinape, Natawe and Okahsa: in sequential order upriver), though the best section is situ-

ated at the base of the Hunstein Range between Gahom and Okahsa, close to the junction of the April and Sitipa rivers (Figs. 3, 4). A conspicuous feature of the hill community is the presence of *Agathis labillardieri* Warb. emergents on the ridge buttresses and crestlines. *Agathis* attains heights exceeding 50 m, and the April provenances can be seen from the river towering over the surrounding canopy. The populations are of commercial significance, so not unexpectedly, has attracted the attention of logging and ecoforestry operators. Due to the steep and rocky slopes, Bugabugi villagers do not establish subsistence gardens in the foothill habitat, and the slopes are thus remarkably free of human disturbance. However, many understories near the river are being disrupted by domestic and wild pigs. Large seral gaps are also scattered through the forest as a result of natural disturbances from landslides, lightning strikes, and windthrows. For a lowland environment, the frequency of lightning-induced gaps is surprisingly high, an indication of the intense electrical and thunderstorm activity in the Hunstein Range.

During the 1998 el Niño disturbance, the Hunstein subdistrict and the entire basin to the south was severely affected by drought. The Sepik became dry in many sections even though it represents the largest catchment system among PNG's rivers. At Yambon gate, the Sepik current normally accelerates through a narrow channel renowned for treacherous whirlpools (cf. Townsend 1968), yet villagers were able to walk across to the opposite bank during the 1998 drought. In spite of such conditions, and unlike many other forested sites in PNG, April River environments did not experience any fires during the last disturbance. However a large tract downstream of Bitara has been recently flattened by cyclonic-force winds, and the forest canopy in a swath ca. 1 km wide completely removed. From current events, it is apparent that vegetational histories in this basin are at least partly determined by catastrophic events (cf. Johns 1986).

Since the time of its initial exploration, the Hunstein subdistrict has been judged a particularly significant hotspot for diversification and endemism. The biodiversity status of the area has assumed legendary proportions, even though the perception of unusual richness can be regarded as a natural outcome of physical and historical considerations.

The geological complexity of the April-Hunstein territory is a major contributing factor in the diversification of its flora. Alluvium, colluvium, sandstone, shale, mafic/ultramafic metamorphics, igneous, clay, and coralline lime

---

[3]Bugabugi is 11–12 km NE of the classical locality of Etappenberg, the latter representing one of Ledermann's collection sites on Kamelsrücken (Camel Back; on some maps now as Samsai Mt) of the Aprilfluss itinerary. Kamelsrücken is known to the Bugabugi people as Oopay. There is some inconsistency in the use of the location name 'Samsai' or 'Samsait', because the name is applied by Wagu and some Bugabugi villagers to Mt. Hunstein (Hunsteinspitze), and is used with that reference, for example, in the Hoogland and Craven collections from 1966.

FIG. 3. Exterior view of the forest at Okahsa. Foreground: April River. The serpentine zone encompassing Okahsa and the south-descending foothills have never been properly explored. Although many plot studies and botanical surveys have been concluded in PNG during the last ten years, there is still not even one floristic account for communities on ultrabasics.

stone substrates occur throughout the area in patches of varying size (Davies & Hutchison 1980a, b). There is thus a highly fragmented pattern of contrasting substrates over the terrain, reflecting the manifold geological origins of the present territory and capable of supporting specialist taxa in a complex mosaic. Superimposed on the foundation of edaphic environments is an exceptional annual rainfall estimated at 7,000–9,000 mm (ibid.). High rainfalls are directly related to floristic diversification (Gentry 1988) so perhumid conditions in the April basin have probably played a major role in the development of a speciose flora. When the dynamic fragmentation of the ecosystem is then considered, over presently observable scales ranging from lightning strikes to catastrophic storms, it is not difficult to imagine how a great number of plant species can be accommodated in side by side fashion over relatively small distances. The heterogeneity of April habitats also needs to be viewed in terms of the evidence regarding correlations between plant distributions and phases of tectonic accretion (cf. Welzen 1997). Part of the district's reputation as a zone of floristic peculiarity (Veldkamp et al. 1988) is due to its easternmost position in the terrane complex which constructed most of northern West Papua (cf. Pigram & Davies 1987). The Hunstein flora is probably best understood as an extension of the West Papuan flora. During the time of Davies and Hutchison (1980b) the Hunstein-April-Salumei petrology was already known to extend

FIG. 4. Interior perspective of the ultramafic forest at Okahsa. Small trees with depauperate crowns are typical of such substrates. Stem densities are high.

westwards rather than eastwards. If the division between PNG and West Papua were to be based on geophysical rather than political criteria, the border would be at April-Salumei rather than Sandaun.

Based on the relationship to tectonics, future distributional records of Hunstein/April endemics will occur to the west, as the Papuan affinity clarifies through further exploration of West New Guinea (Indonesian West Papua). At present, the Indonesian side is even more inadequately surveyed than PNG, and the historical disparity in documentation between the two halves is partly responsible for the perception of unusually high endemism in the Hunstein/April region. The newly discerned disjunction of *Myrmephytum* in the Vogelkop and Hunstein areas (Jebb pers. comm.), of *Faika* in West Papua and the April River (Takeuchi & Renner 2002), and the probable occurrence of *Gyrinops ledermannii* in Jayapura (Takeuchi & Golman 2002) are suggestive of the phytogeographic connections, and of the effect which historical patterns in floristic documentation have on assumed distributions (Figs. 5, 6).

DISCUSSION

Nearly 90 years after the Kaiserin Augusta Expedition, many of the environments along the April River are still unexplored. The localities at the Expedition's farthest penetration into the south basin, near the headwaters of the Bamali tributary, have never been revisited. Of these, Lordberg is probably the most intriguing, but any effort focused on the Divide south of Niksak will undoubtedly reap huge rewards. The recent discoveries from Bugabugi exemplify the possibilities. Although the 6,639 collections taken by Ledermann represent an unprecedented achievement for his time, even a personal effort of that intensity cannot provide the desired level of sampling saturation for such a floristically rich region. A collections program delivering at least 10,000 new numbers is much needed.

The factors militating in favor of future survey success in the April drainage can be recanted: 1) forest communities in the region are in an exceptional state of preservation, 2) traditional lifestyles and ethnobotanical competences are still retained by local villagers, who are thus a valuable source of the folklore knowledge being rapidly lost in other districts, 3) improved site access to the interior basin will enable adoption of cost-effective logistical schedules, 4) research conducted by various investigators since 1989, has created local awareness of the work done by scientists, which will facilitate future inventories.

No collections effort conducted under normal constraints, can achieve 100% coverage of a targeted flora. There is always something which will be overlooked on account of rarity, phenology, localized distribution, logistical limitations, etc. Even the collections obtained by Ledermann during his Sepik travels are not such a superlative effort as may appear at first glance. The 6,600+ numbers from the Kaiserin Augusta survey amount to approximately 400 numbers per

FIG. 5. *Faika villosa* (Kaneh. & Hatus.) Philipson, in the forest understory at Okahsa (det. by S.S. Renner).

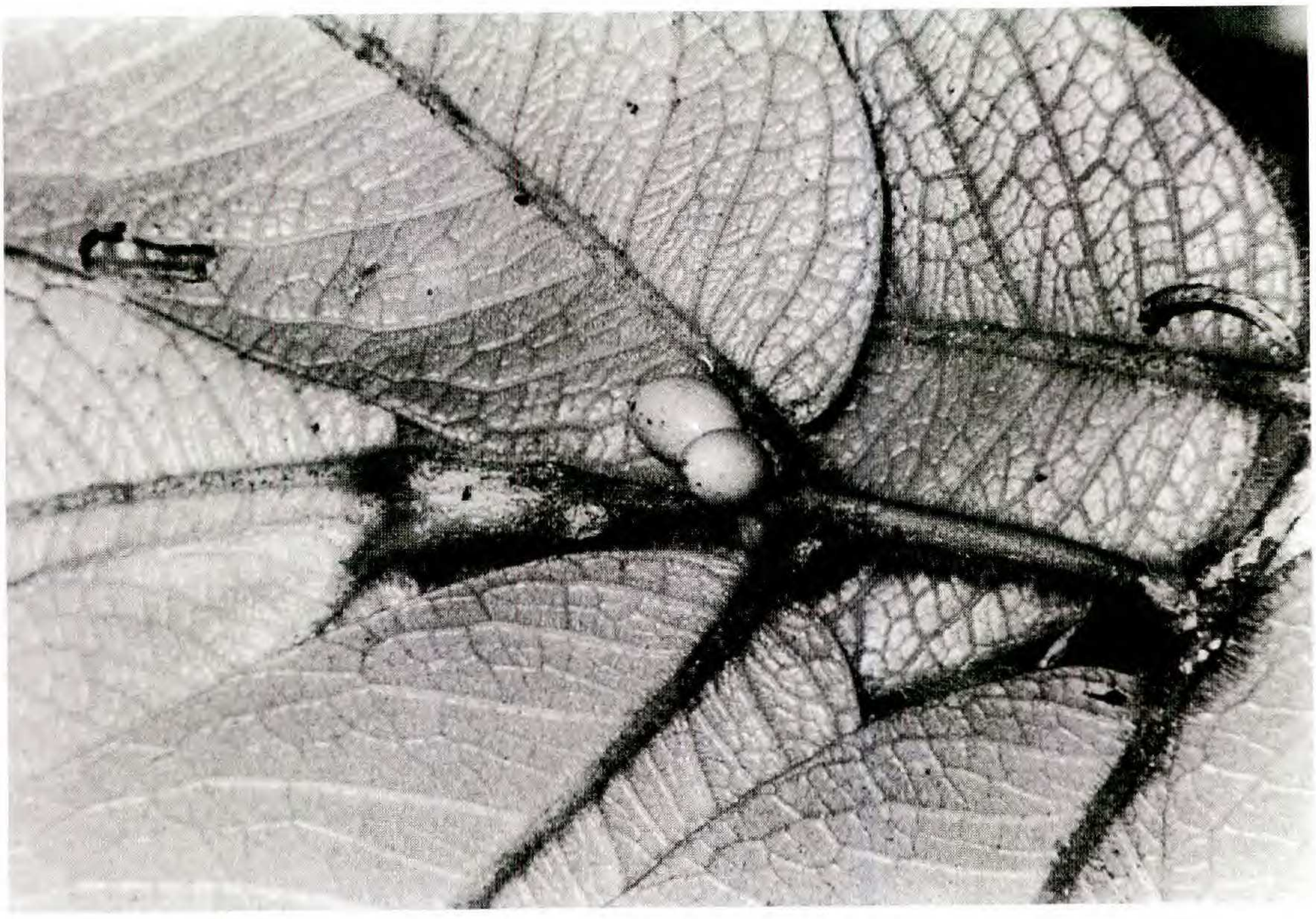

FIG. 6. As for figure 5, showing leaves, branchlet, and fruits (leaf blades ca. 10 cm wide). The April River *Faika* occurrences are a PNG generic record in Monimiaceae (cf. Takeuchi & Renner 2002).

month on a time-averaged basis (excluding Ledermann's 2 months of inactivity due to sickness). By the productivity standards of contemporary collectors working under rapid assessment protocols, this is a below-average result. The significance of the Ledermann collections are another matter altogether however. And in fairness, the logistical environment of his time was undoubtedly much more limiting than now. The difficulties of prolonged expeditionary schedules also should not be underestimated. Anyone with knowledge of Papuasian forest environments can appreciate the hardships in being exposed to tropical conditions for the duration which Ledermann was subjected to.

Some indication of the spottiness of Ledermann's sampling coverage can be gauged by results from the 1966 and 1989 expeditions to Mt. Hunstein. Several scores of new taxa have been described from the later visits, so clearly the original effort was not very comprehensive. To what extent does that situation apply to even more remote sites, such as Niksak-Lordberg? On the basis of accumulating evidence showing that the richest floristic interval in Papuasia is the premontane zone (Takeuchi & Golman 2001), the best environments within the April region are probably the ones at the Central Divide, and these have never been seen since Ledermann's time. The diversity potential of this flora has yet to be plumbed.

ACKNOWLEDGMENTS

We thank parataxonomist A. Towati of Ambunti, the Glei villagers of Waskuk, and the Galiase and Kokomo clans, for their assistance during our visits to the upper Sepik. Hitofumi Abe (Ecosystem Research Group, University of Western Australia) wrote the Japanese translation. Figure 1 was adapted from Geographic Information System downloads from the PNG Forest Authority. Reviewers David Middleton (Harvard University Herbaria) and an anonymous referee, made helpful comments on the draft.

REFERENCES

Allen, G.R. 1991. Field guide to the freshwater fishes of New Guinea. Christensen Research Institute Publ. 9:1–268.

Davies, H.L. and D.S. Hutchison. 1980a. Papua New Guinea 1:250,000 geological series map. Ambunti, sheet SB 54-4. Geological Survey of Papua New Guinea, Dept. Minerals and Energy.

Davies, H.L. and D.S. Hutchison. 1980b. Explanatory notes to accompany the Ambunti 1:250,000 geological map. Report 80/1. Geological Survey of Papua New Guinea, Dept. Minerals and Energy. Pp 1–25.

Ding Hou. 1960. Thymelaeaceae. Flora Malesiana ser. I, 6 (1):1–48.

Gentry, A. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann. Miss. Bot. Gard. 75: 1–34.

Gideon, O.G. 1998. Systematics and evolution of the genus *Tapeinochilos* Miq. (Costaceae-Zingiberales). Ph.D. thesis. James Cook University of North Queensland, Australia.

Hammermaster, E.T. and J.C. Saunders. 1995a. Forest resources and vegetation mapping of Papua New Guinea. PNGRIS Publ. 4, Canberra, CSIRO and AIDAB.

Hammermaster, E.T. and J.C. Saunders. 1995b. Forest resources and vegetation mapping of Papua New Guinea. 1:250,000 vegetation map overlays separately issued as working copies to PNGRIS Publ. 4, Canberra, CSIRO and AIDAB.

Johns, R.J. 1986. The instability of the tropical ecosystem in New Guinea. Blumea 31:341–371.

Louman, B. and S. Nicholls. 1995. Forestry in Papua New Guinea. In: N. Sekhran and S. Miller, eds. Papua New Guinea country study on biological diversity. Colorcraft Ltd, Hong Kong. Pp 155–167.

National Statistical Office. 2001. Papua New Guinea 2000 census preliminary figures. In: Weekender Post Courier. August 3, 2001: 10–11.

Paijmans, K., (ed.) 1976. New Guinea vegetation. CSIRO and Australian National University Press, Canberra.

Papua New Guinea Forest Authority. 1998. Forest resource acquisition general information. PNG Forest Authority.

Pigram, C.J. and H.L. Davies. 1987. Terranes and the accretion history of the New Guinea orogen. J. Austr. Geol. Geoph. 10:193–211.

SOHMER, S.H., R. KIAPRANIS, A. ALLISON, and W. TAKEUCHI. 1991 (unpublished). Report on the Hunstein River expedition – 1989. Pp 1–70.

STEENIS-KRUSEMAN, M.J. VAN. 1950. Malaysian plant collectors and collections. Being a cyclopedia of botanical exploration in Malaysia and a guide to the concerned literature up to the year 1950. Fl. Male. ser. I, 1:1–639.

TAKEUCHI, W. and M. GOLMAN. 2002. The identity of eaglewood (*Gyrinops*, Thymelaeaceae), a new economic resource for Papua New Guinea. Sida 20:261–267.

TAKEUCHI, W. and S.S. RENNER. 2002. A generic record for *Faika* (Monimiaceae) in Papua New Guinea. Fl. Male. Bull. 13:54–55.

TOWNSEND, G.W.L. 1968. District officer, from untamed New Guinea to Lake Success, 1921–46. Pacific Publications, Sydney, 1–271.

VELDKAMP, J.F., W. VINK, and D.G. FRODIN. 1988. XI. Ledermann's and some other German localities in Papua New Guinea. Fl. Male. Bull. 10: 32–38.

WARNER, J.N. and C.O. GRASSL. 1958. The 1957 sugar cane expedition to Melanesia. Hawaiian Planters' Record 55:209–236.

WELZEN, P.C. VAN. 1997. Increased speciation in New Guinea: tectonic causes? In: J. Dransfield, M.J.E. Coode, and D.A. Simpson, eds. Plant diversity in Malesia III. Proceedings of the Third International Flora Malesiana Symposium 1995. Pp 363–387.

BIOSYSTEMATIC ANALYSIS OF THE *THELESPERMA SUBNUDUM* COMPLEX (ASTERACEAE)

Curtis J. Hansen[1] and Loreen Allphin[2]

Department of Botany and Range Science
Brigham Young University
Provo, UT 84602, U.S.A.

Michael D. Windham

Garrett Herbarium
Utah Museum of Natural History
University of Utah,
Salt Lake City, UT 84112, U.S.A.

ABSTRACT

Chromosome studies and phylogenetic analyses of morphology, allozymes, and nrDNA-*ITS* sequence data were used to resolve taxonomic relationships in the *Thelesperma subnudum* complex. Of special interest is the placement of three globally rare members of the complex: *Thelesperma caespitosum*, *T. pubescens*, and *T. subnudum* var. *alpinum*. The first two rare taxa yield only diploid (*n*=12) chromosome counts; *T. subnudum* var. *alpinum* is consistently tetraploid (*n*=24). *Thelesperma subnudum* var. *subnudum* exhibits both diploid (*n*=12) and tetraploid (*n*=24) populations. Phylogenetic analyses of individual data sets strongly support (bootstrap 88%–99%) *T. subnudum* var. *alpinum* as being more closely related to *T. pubescens* and *T. caespitosum* than to *T. subnudum* var. *subnudum*. Combined analyses give the strongest support (bootstrap 100%) for the clade of *T. pubescens*, *T. caespitosum*, and *T. subnudum* var. *alpinum*. Preliminary evidence suggests that *T. subnudum* var. *alpinum* may be an allotetraploid resulting from hybridization between *T. pubescens* and *T. subnudum*. Based on the available evidence, we propose the following nomenclatural changes: ***Thelesperma pubescens*** Dorn var. ***caespitosum*** (Dorn) C.J. Hansen, stat. nov., and ***Thelesperma windhamii*** C.J. Hansen, nom. et stat. nov.

KEY WORDS: *Thelesperma*, Asteraceae, nrDNA-*ITS* sequences, phylogenetics, and systematics.

RESUMEN

Se han usado estudios cromosómicos y análisis filogenéticos de datos morfológicos, alozimas y de secuencias de nrDNA-ITS para tratar de resolver las relaciones taxonómicas dentro del complejo *Thelesperma subnudum*. De especial interés es la posición taxonómica de los tres miembros del complejo: *Thelesperma caespitosum*, *T. pubescens* y *T. subnudum* var. *alpinum*, considerados globalmente raros. Los dos primeros taxa mostraron solamente poblaciones diploides (*n* = 12), mientras que *T. subnudum* var. *alpinum* se mostró constantemente como tetraploide (*n* = 24). *Thelesperma subnudum* var *subnudum* mostró tanto poblaciones diploides (*n* = 12) como tetraploides (*n* = 24). Los resultados del análisis filogenético de diferentes tipos de datos soportan más fuertemente (bootstrap 88%–99%) el agrupamiento de *T. subnudum* var. *alpinum* con *T. caespitosum* y *T. pubescens*, que su agrupamiento con *T. subnudum* var. *subnudum*. Los análisis combinados mostraron el máximo soporte (bootstrap 100%) para el clado compuesto por *T. subnudum* var. *alpinum*, *T. caespitosum* y *T. pubescens*. Evidencias preliminares sugieren que *T. subnudum* var. *alpinum* podría ser un alotetraploide resultante de la hibridación entre *T. subnudum* y *T. pubescens*. De acuerdo con la evidencia disponible proponemos los siguientes cambios nomenclaturales: ***Thelesperma pubescens*** Dorn var. ***caespitosum*** (Dorn) C.J. Hansen, stat. nov. y ***Thelesperma windhamii*** C.J. Hansen, nom. et stat. nov.

PALABRAS CLAVE: *Thelesperma*, Asteraceae, nrDNA-*ITS* secuenciación, filogenética y sistemática.

[1]Current Address: Biological Sciences Department, Auburn University, Auburn, AL 36849, U.S.A.
[2]Author for correspondence: (email; loreen_woolstenhulme@byu.edu)

Thelesperma Lessing (Asteraceae: Heliantheae, Coreopsidinae) comprises about 15 species, mostly herbaceous perennials (annuals and subshrubs rare), native to south-central and western North America and warm-temperate South America (Melchert 1963; Bremer 1994a). The genus is thought to be monophyletic based on shared characters such as strongly dimorphic involucral bracts, scarious-margined inner involucral bracts that are connate from 1/5 to 1/2 their lengths, opposite leaves, and pappi that are absent or composed of hispid or serrulate awns (Bremer 1994a). Previous taxonomic studies of *Thelesperma* have focused on morphology (Shinners 1950a, b; Alexander 1955) and cytology (Melchert 1963; Greer 1997; Greer & Powell 1999) and were not explicitly phylogenetic. Nevertheless, past work on the genus has identified some species groups that may be monophyletic. One of these is the *Thelesperma subnudum* complex, which is restricted to the Colorado Plateau and areas adjacent to the Rocky Mountains in western North America (Fig. 1). This group includes five commonly accepted taxa: *T. subnudum* A. Gray var. *subnudum*, *T. subnudum* A. Gray var. *alpinum* S.L. Welsh, *T. pubescens* Dorn, *T. caespitosum* Dorn and *T. marginatum* Rydb. Features used to distinguish members of the *T. subnudum* complex are given in Table 1.

Delimitation of taxa within the *Thelesperma subnudum* complex has varied, and at least three classifications have appeared (Table 2). Dorn (1990), who discovered and named *T. pubescens* and *T. caespitosum*, recognized each as distinct species. He treated *T. marginatum* as a separate species and accepted *alpinum* as a variety of *T. subnudum*. In the 2nd edition of *A Utah Flora*, Welsh et al. (1993) classified both *T. caespitosum* and *T. subnudum* var. *alpinum* as varieties of *T. subnudum*; *T. marginatum* and *T. pubescens* were not treated because the former is not known from Utah and discovery of the latter in Utah postdates publication of the flora. Cronquist et al. (1994) recognized only *T. subnudum* and *T. pubescens* at the species level; *T. caespitosum* and *T. subnudum* var. *alpinum* were included within *T. pubescens*, and *T. marginatum* was treated as a variety of *T. subnudum*.

These divergent classifications result from differing interpretations of the available morphological and cytological information. Additional genetic data (e.g., allozyme and DNA) are needed to allow an informed choice between competing taxonomies. The need to pursue these studies has been heightened recently by conservation concerns. *Thelesperma pubescens*, *T. caespitosum*, and *T. subnudum* var. *alpinum* are rare taxa restricted to a few localized populations (Fig. 1). All three have been listed as potentially endangered (category 2) by the U.S. Fish and Wildlife Service (U.S. Dept. of Interior 1985, 1993). The accumulation of genetic data is an important step in determining their eligibility for federal protection under the Endangered Species Act.

Our objectives in this study are threefold: 1) to develop baseline genetic data for members of the *Thelesperma subnudum* complex, 2) to analyze the data in

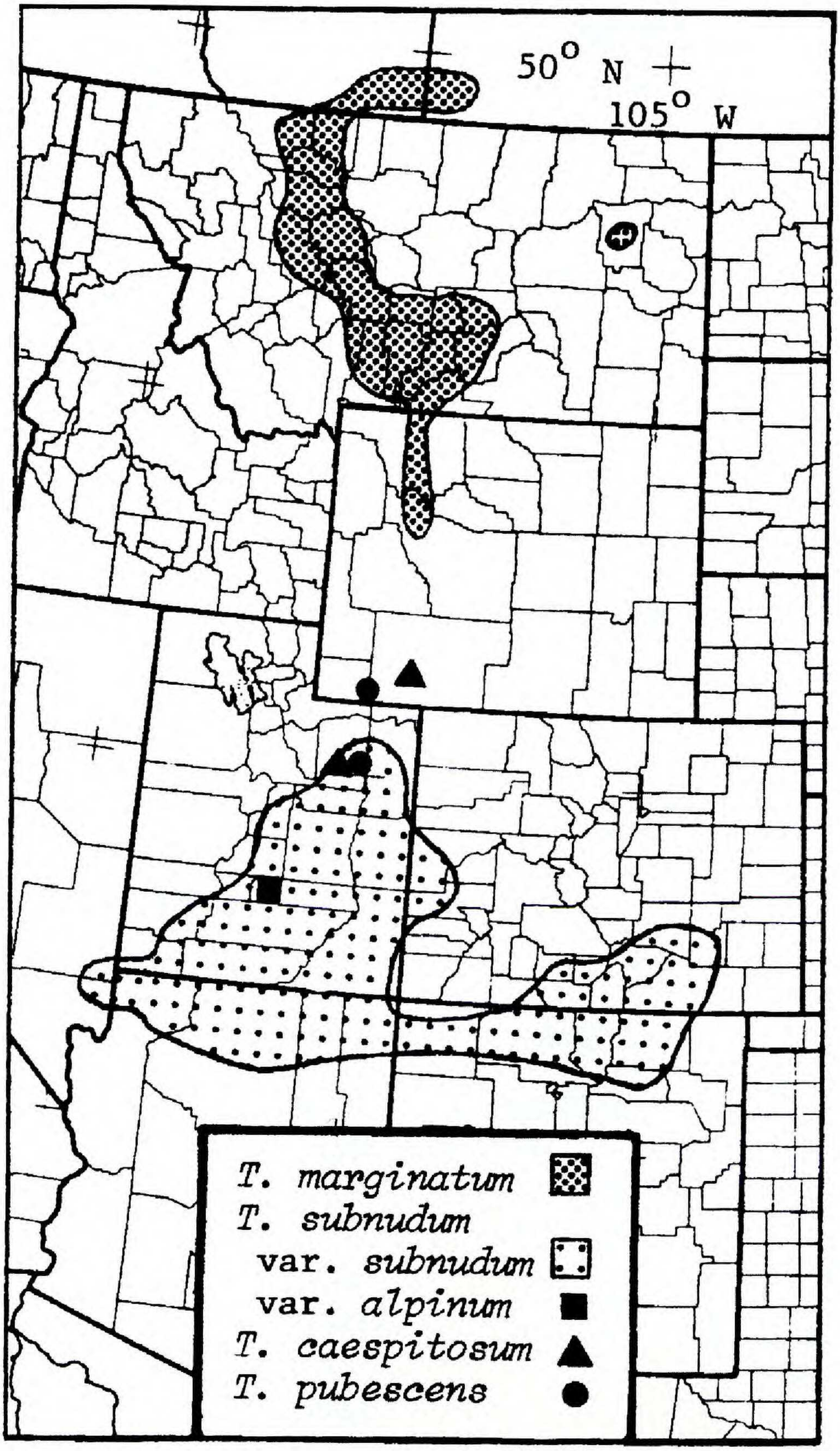

FIG. 1. Distribution of taxa in the *Thelesperma subnudum* complex. (Modified from Dorn 1990).

TABLE 1. Selected morphological, ecological, and distributional features distinguishing taxa of the *Thelesperma subnudum* complex. Modified from Dorn 1990.

Taxa	Leaf segments	Pubescence	Heads	Rootstock	Habitat	Elevation (m)
T. subnudum	long, broad	none	1-several, radiate (rarely) discoid	somewhat creeping	common, sandy soils	1050–2310
T. subnudum var. *alpinum*	short, narrow	lower stems & leaves	1(2), discoid	somewhat creeping, branched caudex	specialized, Carmel Form. Navajo Sandstone	1830–2680
T. marginatum	long, broad	none	1-several, discoid	somewhat creeping	common, sandy out wash	2130–2835
T. pubescens	short, narrow	leaves	1(2), discoid	branched caudex	specialized, weathered Bishop conglomerate	2430–2715
T. caespitosum	short, narrow	petioles (lower blade)	1(2), discoid	branched caudex	specialized, whitish shale	1220–2680

concert with morphology to produce an explicit phylogenetic hypothesis for these taxa, and 3) to compare that hypothesis to existing classifications and propose any desirable taxonomic changes. Through this process, we hope to shed light on the relationships and possible origin of *T. subnudum* var. *alpinum*, the rarest and most enigmatic member of the group.

MATERIAL AND METHODS

Determination of Chromosome Numbers/Ploidy Level

Ploidy levels were determined for all taxa in the *T. subnudum* complex using a combination of chromosome counts and analyses of allozyme banding patterns. For chromosomal observations, capitula (in bud) were obtained from field populations and fixed in Farmer's solution (3 parts ethanol:1 part glacial acetic acid). Chromosome counts were made from meiotic figures obtained using standard squash techniques and acetocarmine staining (Turner & Johnston 1961; Strother 1972). Preparations were examined under phase contrast on a Zeiss Axioplan2 Microscope. Images of chromosome squashes were saved electronically using Zeiss Image® software from Carl Zeiss, Inc.

In populations for which flower buds were unavailable, ploidy level was determined by careful examination of allozyme banding intensities across a variety of enzymes (Danzmann & Bogart 1982a; Dessauer & Cole 1984; Pryer & Haufler 1993). Because allozyme markers are additive, codominant, and

TABLE 2. Previous taxonomic treatments of *Thelesperma subnudum* and allied taxa.

Dorn (1990)	Welsh et al. (1993)	Cronquist et al. (1994)
T. subnudum var. *subnudum*	*T. subnudum* var. *subnudum*	*T. subnudum* var. *subnudum*
T. subnudum var. *alpinum*	*T. subnudum* var. *alpinum*	*T. pubescens*
T. pubescens	Not treated	*T. pubescens*
T. caespitosum	*T. subnudum* var. *caespitosum*	*T. pubescens*
T. marginatum	Not treated	*T. subnudum* var. *marginatum*

inherited in a Mendelian fashion, the expressions of alleles at various ploidy levels are expected to be proportional to their gene dosages. In our study, chromosomally documented diploids in *Thelesperma* always showed balanced band patterns at heterozygous loci. If a heterozygote showed unequal band intensities of 3:1 (in a monomeric enzyme) or 9:4:1 (in a dimeric enzyme), the particular individual always proved to be tetraploid (the only type of polyploid encountered during our study). Thus, chromosomally unknown populations could be assigned to a specific ploidy level based on the presence or absence of unbalanced heterozygous allozyme patterns.

Morphological Data

Our coding of morphological character states is based on observation of approximately 300 herbarium sheets from ASC, BRY, GH, MONTU, NMU, NY, RM, UT, and UTC (herbarium designators follow Holmgren et al. 1990). These data were supplemented by information obtained from Melchert (1963), Welsh (1983), Dorn (1983, 1990), Jansen et al. (1991), Ryding & Bremer (1992), Welsh et al. (1993), Cronquist et al. (1994), and Karis & Ryding (1994). Ingroup taxa included *T. subnudum* var. *subnudum*, *T. subnudum* var. *alpinum*, *T. pubescens*, *T. caespitosum*, and *T. marginatum*, plus the related species *T. filifolium* (Hook.) A. Gray, *T. longipes* A. Gray, and *T. megapotamicum* (Spreng.) Kuntze. *Bidens* has been identified as a possible sister genus to *Thelesperma* (Ryding & Bremer 1992) and two species of that diverse genus, *B. cernua* L. and *B. frondosa* L., were chosen as outgroup taxa. A total of 16 characters (14 binary and 2 multi-state) was included in the morphological analysis (Tables 3, 4).

nr DNA-ITS Sequence Data

Samples used in the DNA study are identified by their GenBank accession numbers in Table 5. *ITS* sequences for the outgroups *Bidens cernua* and *B. frondosa* were obtained from GenBank; voucher data for these collections can be found in Ganders et al. (2000). The *ITS* sequences for all *Thelesperma* taxa were obtained directly by extracting total DNA from the leaf tissue of dried specimens using a basic CTAB extraction protocol (Hillis et al. 1996). Two different individuals from each taxon were sampled in order to check for intraspecific differences. The *ITS*-1 & 2 and 5.8S regions were amplified using the polymerase chain